PRAY, T. R. 1968. Interpopulation variation in the gametophytes of Pellaea andromedaefolia (Kaulf.) Fée. (manuscript).
TRYON, A. F. 1957. A revision of the fern genus Pellaea section Pellaea. Ann. Mo. Bot. Gard. **44:** 125–193.
———. 1960. Observations on the leaves of Pellaea andromedaefolia. Contr. Gray Herb. **187:** 61–68.

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Petiolar Shoots in the Dennstaedtioid and Related Ferns[1]

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Stelar branching patterns and bud formation in the Filicales have been investigated little since the beginning of this century. Fern stems may branch by dichotomy, axillary buds, or buds not clearly in the axils of leaves. Buds from frond bases were reported and described by Gwynne-Vaughan (1903) for a number of ferns. In a monographic work on *Dennstaedtia punctilobula* (Michx.) Moore, Conard (1908) described in detail the anatomy of shoots from the petiole bases of this fern. Webster (1958) observed dormant buds on the leaf bases in *Pteridium aquilinum* var. *latiusculum*, but none were seen to elongate. Further references to budding of ferns are scattered, and the phenomenon is mentioned only briefly, as in Wardlaw (1952) and Wagner (1963), for *Matteuccia*, *Onoclea* and *Dryopteris*. None of these workers has attributed any phylogenetic or taxonomic importance to the phenomenon, and, in view of the meager information available, it is appropriate that more comprehensive studies be undertaken.

In the summer of 1967 we participated in a course in the biology of tropical pteridophytes offered by the Organization for

[1] This study was done while the senior author held a National Defense Education Act Fellowship. Partial cost of publication of this paper was borne by the Smithsonian Institution while the junior author was a National Research Council Visiting Research Associate in the Department of Botany of the Smithsonian Institution.

Tropical Studies in Costa Rica (Mickel, 1967), in which we had the opportunity to investigate a great diversity of fern genera and species in regard to their branching patterns. This study is based upon free-hand sections of rhizomes and petiole bases examined under a dissecting microscope. The results show that the phenomenon of petiolar branching occurs more commonly in the ferns than was thought previously (*Table I*). This branching is very widespread in the dennstaedtioid ferns, being a nearly constant feature in *Dennstaedtia*, *Hypolepis*, *Paesia*, and *Histiopteris*, less constant in *Pteris*, and absent in *Saccoloma*. Also in the Cyatheaceae petiole branches are always present in *Lophosoria* and *Cyathea mexicana*, and occasionally so in *Dicksonia* and *Metaxya*. One species of *Dicksonia* studied had up to six buds on the lower stipe. *Metaxya* is reported (Bower, 1928) to bud from the petiole base, but our specimen did not.

In most of the ferns studied, the vascular strand to the frond begins as a bulging of the rhizome stele (*Figs. 1* and *3*), followed by its breaking away from the stele and passing out through the cortex. In all the ferns studied the frond trace retains a basic horseshoe shape with the additions of hooks, corrugations, and dissections in various species. The gap left in the rhizome stele by the departing frond is then closed. The rhizomes of some species possess a dicyclic (or rarely tricyclic) solenostele. In these plants the closure of the frond gap may be accomplished by a portion of the inner stele filling the outer. The whole inner solenostele may migrate to the gap, leave a filling portion, and center again as it closes its own gap (*Fig. 3*); or the section which will fill the outer stele may depart from the inner stele and migrate to the gap (*Fig. 2*). If there is a third solenostele, it repeats the pattern of the second.

The bud develops well up on the stipe, at least after the leaf trace has become well differentiated from the rhizome stele (*Fig. 1*). (One exception to this was in *Cyathea* where the bud develops with the petiole trace but appears superficially to be on the stem to one side of the leaf base.) The adaxial hook of the petiolar strand lengthens laterally and separates from the

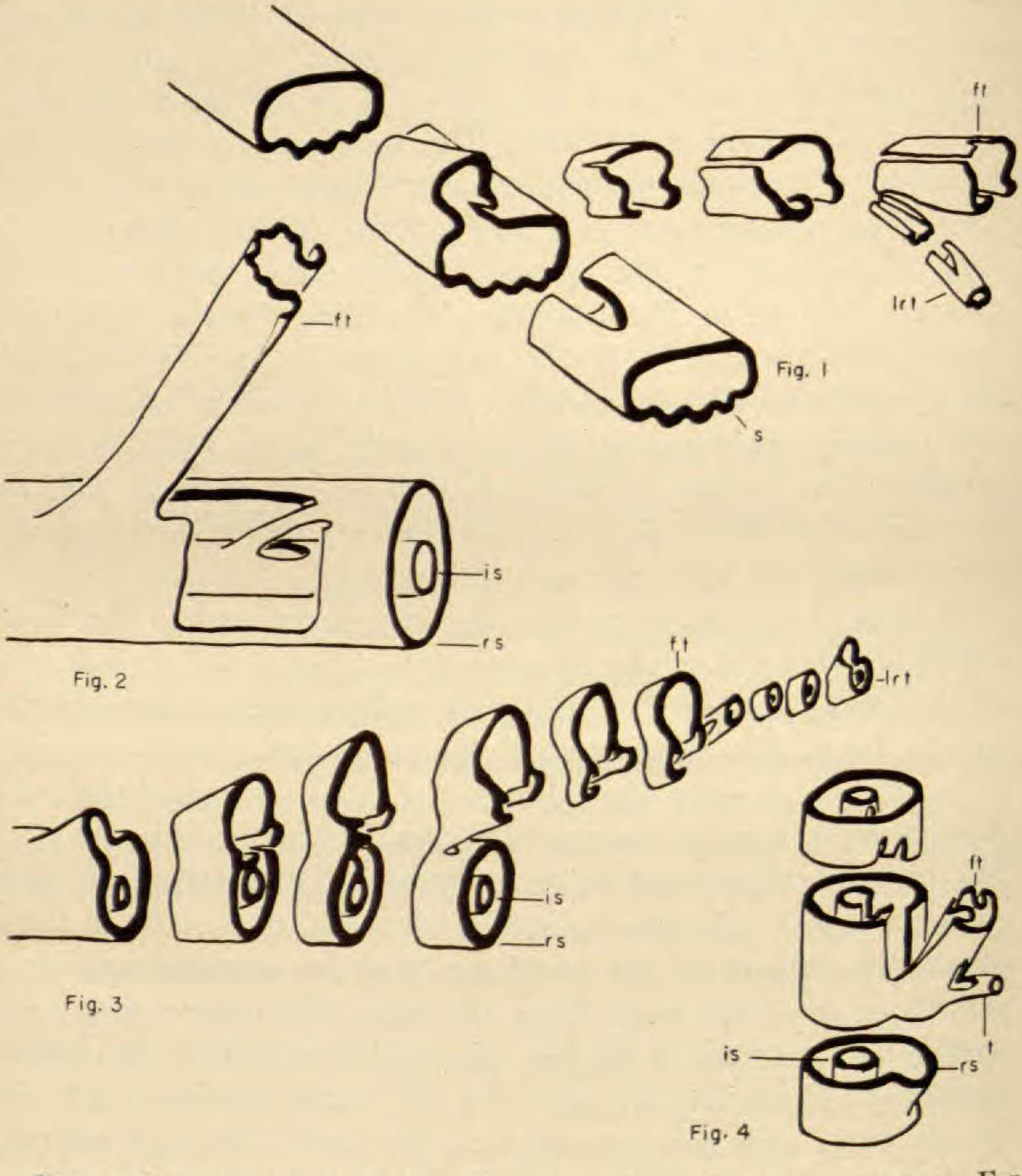

FIG. 1. EXPLODED DIAGRAM OF HYPOLEPIS REPENS STELAR SYSTEM. FIG. 2. SACCOLOMA INAEQUALE STELAR SYSTEM. FIG. 3. EXPLODED DIAGRAM OF DENNSTAEDTIA DISSECTA VASCULAR SYSTEM. FIG. 4. EXPLODED DIAGRAM OF PTERIS ALTISSIMA VASCULAR SYSTEM. The abbreviations are: ft = FROND TRACE, is = INNER RHIZOME STELE, lrt = LATERAL RHIZOME TRACE, rs = OUTER RHIZOME STELE, s = RHIZOME STELE, and t = ABAXIAL PETIOLAR BRANCH.

frond stele, gradually closing into a new solenostele. The frond stele reforms the adaxial hook. In the dicyclic condition the inner stele of the lateral shoot may repeat the ontogeny of that of the main rhizome. This was found in *Pteris* and some species of *Dennstaedtia*. In other dicyclic species, however, the inner stele forms by an invagination of the outer stele, which separates and moves into the center closing into a solenostele (*Fig. 3*).

There are but few generic differences from the above general pattern. The species of *Hypolepis* investigated are fairly uniform in their anatomy with usually dorsiventral rhizomes, unicyclic solenosteles and petiolar branches. There are usually two to four petiolar buds, often well-developed and growing as lateral branches bearing fronds. *Histiopteris incisa* is scarcely distinguishable from *Hypolepis* in its stelar anatomy; the two are closely allied.

All the Dennstaedtias examined bore lateral shoots on the petioles (usually one per petiole), whereas only two species (*D. bipinnata* and *D. cicutaria*) displayed dichotomizing rhizomes. *Dennstaedtia bipinnata* is the only unicyclic species studied. *Dennstaedtia cicutaria* exhibits a most peculiar pattern. The rhizome appears to terminate in a trichotomy consisting of a central petiole and two rhizome branches. Since this type of branching pattern is found in no other species examined and only irregularly in *D. cicutaria*, it seems likely that the rhizome has branched dichotomously while a petiole was produced simultaneously.

Some ferns form buds in positions other than at the adaxial petiole trace hooks. The fronds of both *Pteris podophylla* and *Pteris altissima* produce buds from the abaxial side of the petiole strand (*Fig. 4*). This position also has been found in three species of Costa Rican *Grammitis* (L. E. Bishop, pers. comm.). The bud in *Dicksonia* develops from the lateral vascular arc, and in *Lophosoria* bud formation occurs on the lateral side of the abaxial strand. The bud trace of *Paesia* arises from both adaxial and abaxial portions of the petiole trace, one section from the adaxial hook and two sections from the abaxial corrugated arc. These three strands unite to form the lateral branch. The ability of the petiole

trace to form a rhizome stele is not limited to a specific portion of the petiole.

The petiolar branching discussed above resembles that of certain coenopterid ferns of the Carboniferous Age. *Botryopteris* and *Anachoropteris* are well-known examples in which branches often arise from the petioles. Surange (1952) interprets the anatomy of *Botryopteris* as a dorsiventral stem giving rise to a terete stem upon which petioles and roots are borne. Delevoryas and Morgan (1954) discuss the phenomenon of stems arising from

TABLE I. RHIZOME CHARACTERISTICS IN DENNSTAEDTIOID AND RELATED FERNS.

Name	*Stelar cycles*	*Dichotomies*	*Petiolar branches*
Blotiella lindeniana (Hook.) Tryon (*3432*)[1]	1	—	+
Culcita coniifolia (Hook.) Maxon (*3238*)	1	−	−
Cyathea mexicana Schlecht. & Cham.	1	−	+
Dennstaedtia arborescens (Willd.) Ekman ex Maxon (*1870*, *2037*, *2045*, *2212*, *2226*, *2305*, *2526*, *2535*, *2589*, *3111*, *3305*)	2	−	+
D. bipinnata (Cav.) Maxon (*2697*, *3345*, *3505*, *3593*, *3616*)	1	+	+
D. cicutaria (Swartz) Moore (*1869*, *2303*, *2914*, *3118*)	2	+	+
D. dissecta (Swartz) Moore (*2209*, *2210*, *2217*, *2224*, *2301*, *2594*)	2	−	+
D. obtusifolia (Willd.) Moore (*1871*, *2302*, *2304*, *2595*, *2631*)	2	−	+
D. spinosa Mickel (*2730*)	2	−	+
Dicksonia gigantea Karst. (*3134*)	1	−	+
Histiopteris incisa (Thunb.) J. Smith (*2182*, *2483*, *3193*)	1	−	+
Hypolepis bogotensis Karst. (*2169*, *3248*)	1	−	+
H. nigrescens Hook. (*3422*)	1	−	+
H. nuda Mett. (*3300*)	1	−	+
H. pulcherrima Underw. & Maxon (*3306*)	1	−	+
H. repens (L.) Presl (*1972*, *2000*, *2306*, *2743*, *3048*)	1	−	+
H. rigescens (Kunze) Fée (*2457*)	1	−	+
H. viscosa (Karst.) Mett. (*3315*)	1	−	+

Name	Stelar cycles	Dichotomies	branches
Lonchitis hirsuta L. (*2293*, *2590*, *3557*)	1	–	–
Lophosoria quadripinnata (Gmel.) C.Chr. (*2431*)	1	–	+
Metaxya rostrata (H.B.K.) Presl (*2853*)	1	–	+
Paesia anfractuosa (Christ) C. Chr. (*3000*)	1	–	+
Pteridium aquilinum var. *arachnoideum* (Kaulf.) Herter (*2017*, *2153*)	2	+	+
P. a. var. *caudatum* (L.) Sadeb. (*2395*)	2	+	+
Pteris altissima Poir.	2	–	+
P. podophylla Swartz (*3177*)	2–3	–	+
P. pungens Willd. (*3563*)	1	–	–
P. quadriaurita Retz.	1	–	–
Saccoloma elegans Kaulf. (*1932*, *2799*)	2	–	–
S. inaequale (Kunze) Mett. *1992*, *2755*, *3128*, *3566*)	2	–	–

[1]The numbers cited are Mickel collection numbers. Voucher specimens are deposited at US, ISC, LP, and USJ. Those without vouchers cited were common species not collected at the time of the study.

petioles, particularly in *Anachoropteris clavata*. They believe that Surange's "dorsiventral stem" is actually a petiole with stems arising from it as in *Anachoropteris*. *Anachoropteris clavata* is postulated as a scrambling plant with some petioles functioning as stolons producing new stems. Other coenopterid ferns are also known to have branching petioles (T. Phillips, pers. comm.).

Among the modern dennstaedtioid ferns several have a habit similar to the above. In *Hypolepis*, for example, the petioles are not entirely erect from the rhizome, but creep for a distance before becoming erect. This horizontal portion bears the branch shoots and closely approximates the condition described by Delevoryas and Morgan. Thus, the patterns of branching and bud formation in these ferns are perhaps more significant than previously believed, for questions are raised regarding the relation of the frond to the rhizome, the basic ontogeny of the frond, and the phylogeny of the dennstaedtioid ferns. Further work on these problems is currently in progress.

LITERATURE CITED

BOWER, F. O. 1928. The Ferns (Filicales), III. Cambridge Univ. Press England.

CONARD, H. W. 1908. The structure and life history of the hay-scented fern Carnegie Inst. Washington. Publ. 94.

DELEVORYAS, T., and J. MORGAN. 1954. A further investigation of the morphology of Anachoropteris clavata. Amer. J. Bot. **41**: 192–203.

GWYNNE-VAUGHAN, D. T. 1903. Observations on the anatomy of solenostelic ferns. Part II. Ann. Bot. **17**: 689–742.

MICKEL, J. T. 1967. An advanced course in pteridophyte biology in Costa Rica. Amer. Fern. J. **57**: 145–161.

SURANGE, K. R. 1952. The morphology of Botryopteris antiqua with some observations on Botryopteris ramosa. The Palaeobotanist **1**: 420–434.

WAGNER, W. H., JR. 1963. Pteridophytes of the Mountain Lake area, Giles County, Virginia, including notes from Whitetop Mountain. Castanea **28**: 113–150.

WARDLAW, C. W. 1952. Phylogeny and Morphogenesis. MacMillan, London.

WEBSTER, B. D., and T. A. STEEVES. 1958. Morphogenesis in Pteridium aquilinum (L.) Kuhn-general morphology and growth habit. Phytomorphology **8**: 30–41.

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Marsilea maheshwarii, a New Species from Pondichery, India

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The genus *Marsilea* is represented in India by nine species,[1] most of which are restricted in distribution, *M. minuta* L. being the only species found throughout India. Endemism is of common occurrence throughout the genus. While examining collections of *Marsilea* from all over the country, I found that some collections

[1] Gupta, K. M. 1962. Marsilea. Botanical Monograph no. 2, C. S. I. R., New Delhi, India.